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Host-Plant Specialisation and Diurnal Dynamics of the Arthropod Community Within *Muhlenbergia robusta* (Poaceae)

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1. Introduction

It is well-known that herbivorous insects are very specialised in terms of their food. It has been reported that these insects feed on only one or a few genera of plants, even within a single family (Bernays & Graham, 1988; Schoonhoven et al., 2005). Certain factors have been found to be decisive in determining the range of hosts of herbivorous insects. Among the most important are (1) the secondary compounds in the plants, (2) the presence of predators, and (3) the insects' mating behaviours. These factors are discussed below.

Secondary compounds are one of the most effective strategies that plants use to avoid predation by herbivores, for example, as toxins or in feeding deterrents that kill insects or slow their rates of development (Lill & Marquis, 2001; Schowalter, 2006). The noxious effects of secondary compounds on insects are crucial to the preferences of feeding insects, and therefore, the ranges of the host plants of phytophagous insects (Bernays & Graham, 1988; Cates, 1980).

Natural enemies can influence the host ranges of phytophagous specialists. Moreover, it has been proposed that species seek out enemy-free spaces to reduce their mortality (Gilbert & Singer, 1975; Lawton, 1978). In fact, Price et al. (1980) recorded insect herbivores that changed their host plant to a new toxic plant that provided protection against enemies.

The literature describes some phytophagous insects that restrict their host range to comply with patterns of mate-finding behaviour. This is true even in plants that do not have a relationship with the food preferences of insects (Labeyrie, 1978).

Conversely, arthropod predators are generalised in their food selection (Sabelis, 1992). For this reason, habitat selection by arthropods depends on the services that the habitat provides to increase their chances of survival. It has been reported that the abundance of arthropod predators within plant communities is related to habitats offering (1) abundant prey; (2) refuge from predation, e.g., cannibalism and intraguild predation; (3) easier and more effective spotting and capture of prey; (4) a more favourable microclimate; and (5) access to alternative resources (Langellotto & Denno, 2004).

In spite of the knowledge gathered about host-plant specialisations within several arthropod species (Bernays & Graham, 1988; Cates, 1980; Feeny, 1976), there is little information about the level of arthropod specialisation in the use of their habitats at the community level (i.e., species that carry out all of their activities on the host plant). Descriptions of arthropod

communities on host plants assume that all species have the same level of specialisation in the use of their habitat. To address this theoretical problem, only the most abundant taxa of the community have been studied. Previous studies about the ratio of arthropods with high specialisation in the use of their habitats are difficult to find. This kind of research could provide important data about the dynamics of the arthropod community on their host plant and about the possible main flows of matter and energy within arthropod-plant ecosystems. The main goals of this study are (1) to determine the ratio of species in the arthropod community in a grass ecosystem (*Muhlenbergia robusta*, Poaceae) with high levels of specialisation in the use of the host plant (i.e., species that carry out all their activities on the host plant), by studying arthropod communities with similar habitats (i.e., herbaceous patches and litter) at four different times throughout the day, and (2) to determine the diurnal variation of the arthropod community structure (richness, abundance, index of diversity and composition) in three different herbaceous habitats (*M. robusta*, herbaceous patches, and litter).

2. Methods

2.1 Area of study

This study was carried out in the Reserva Ecológica del Pedregal de San Ángel (REPSA) (19°19'N, 99°11'W), which is located on the main campus of the Universidad Nacional Autónoma de México, southwest of Mexico City. This ecological reserve has an area of 237 ha and an elevation of 2300 m. The vegetation of the reserve can be characterised as a xerophilous scrubland, and the area has a sub-humid climate. This site has an annual mean temperature of 16.1 °C, and its annual mean rainfall is 835 mm (César-García, 2002). The reserve has a wet season between May and October. The area is located over a basaltic substratum that was deposited 1650 to 2000 years ago during the eruption of the Xitle volcano (Carrillo, 1995). Most plant species are herbaceous or shrub-like; however, there are a few small trees from 3 to 7 m in height.

2.2 Study system

Muhlenbergia robusta (Fourn.) Hitchc. (Poaceae) is a perennial grass 1 to 2 m tall. This plant accounts for approximately 15% of the aboveground net primary productivity in the REPSA (Cano-Santana, 1994). This plant flowers between June and August and bears fruit between September and June (César-García, 2002). It has a distribution between 2250 and 3200 m in elevation (Rzedowski & Rzedowski, 2001).

2.3 Collection

With each collection effort, we had the intention to trap as many arthropods as possible in each of the study habitats; unfortunately, the heterogeneous geomorphology in the REPSA did not allow for the use of the same trapping technique in each habitat. For this reason, the most suitable technique for each kind of habitat (*M. robusta*, herbaceous patches and litter) was used.

Twenty-four *M. robusta* plants – which showed approximately 48 to 73 cm of diameter at ground level – were collected at random at 4 different times of day (0100 to 0300 h, 0700 to 0900 h, 1300 to 1500 h and 1900 to 2100 h). Six grasses were collected during each time period. The collection took place in July 2006 in a large site in the nuclear zone of the REPSA

with the presence of some trees. Each selected grass plant was completely wrapped and protected with a plastic bag in the field and was later extracted using a pick and shovel.

To obtain an authentic epiphytic arthropod community from the herbaceous patches of each grass, an entomological net was struck ten times in the four nearest patches where the herbaceous patches were dominant and *M. robusta* was not present.

To acquire the arthropods associated with a litter habitat, for each plant, the litter of the four nearest patches without vegetation was collected using a 24 cm diameter circle as a sampling unit.

On the same day of the collection, the three habitat samples (*M. robusta*, herbaceous patches, and litter) were taken to the laboratory, where arthropods were manually extracted from them. Only organisms ≥ 3 mm in corporal length were considered. Extracted fauna were initially sorted into morphospecies, a common practice in biodiversity studies that does not compromise scientific accuracy (Oliver & Beattie, 1996) and has some clear advantages when expertise in all taxonomic groups is not available (Gaston, 1996). The morphospecies were identified and then sent to several taxonomists for species identification. The community attributes of each sample were recorded considering richness per plant, abundance per plant, and diversity. Diversity was recorded using the Shannon-Wiener index with a natural logarithm (H').

The aboveground dry weight of each plant was obtained by drying the plant in an electric oven at 50°C to a constant weight, and the plants were then weighed using an analytical balance (Ohaus AV812, ± 0.005 g).

In August 2007, the relative coverages of the principal landscape elements in the site were determined (*i.e.*, *M. robusta*, herbaceous patches, litter, exposed rock, and shrubbery and arboreal plants) using Canfield's method with two lines of 8 m that traversed the site.

2.4 Statistical analysis

To determine the effects of the sampling schedule (0100, 0700, 1300, and 1900 h) and the type of habitat (grass, herbaceous patches and litter) on the community attributes (richness, abundance, and H'), two-way factorial ANOVA were calculated (Zar, 2010). Tukey's multiple comparison tests were then done on significant ANOVA tests. Richness and abundance were transformed using the equation

$$X' = \sqrt{0.5 + X} \quad (1)$$

because they are discrete variables (Zar, 2010). Statistical analyses were conducted with Statistica software (StatSoft, 2007).

To determine the effect of the kind of habitat or the schedules of collection on the composition of arthropod communities, a principal component analysis (PCA) was calculated with Prime software (PRIMER-E, 2001).

To determine the similarity of species composition among the different communities, Jaccard's index of similarity was applied, considering the twelve treatments (four schedules \times three habitats).

3. Results

On the 24 grasses, a total of 139 arthropod taxa and 1529 individuals were found; the herbaceous patch sampling registered 150 arthropod taxa and 1594 individuals; the litter sampling found 60 arthropod taxa and 248 individuals.

Two-way factorial ANOVA tests showed a significant effect of habitat type, the hour of sample collection, and the type of habitat × the hour of collection on richness ($F_{3, 60}=8.1$, $P=0.001$; $F_{2, 60}=84.1$, $P<0.001$; $F_{6, 60}=7.6$, $P<0.001$, respectively), abundance ($F_{3, 60}=3.1$, $P=0.03$; $F_{2, 60}=41.9$, $P<0.001$; $F_{6, 60}=4.1$, $P=0.001$, respectively), and index of diversity ($F_{3, 60}=7.5$, $P<0.001$; $F_{2, 60}=40.4$, $P<0.001$; $F_{6, 60}=4.0$, $P<0.001$, respectively).

Different schedules did not result in significant changes in arthropod mean richness or abundance or in H' in *M. robusta* (Figs. 1A, B, C). In contrast, the lowest richness and abundance averages on the herbaceous patch habitats were at 0100 h. At 0700 h, they showed a sudden increase, and at 1300 h and 1900 h, they showed a slight decrease (Figs. 1A, B). The mean of the arthropod index of diversity was unchanged at different times in the herbaceous habitat patches (Fig. 1C). In the litter habitat, the lowest arthropod richness and diversity averages were at 1300 h, and the highest averages were at 0700 h (Figs. 1A, C). Abundance averages were constant at different times (Fig. 1B).

In the *M. robusta* habitat, the highest average abundance of Formicidae was at 1300 h. Diplopoda, Coleoptera, Hemiptera, Blattodea, and Araneae did not show a clear peak average abundance (Fig. 2A). Orthoptera, Homoptera, Coleoptera, and Diptera showed their lowest average abundance at 0100 h in the herbaceous patch habitat. Later, these taxonomic groups increased their average abundances between 0700 h and 1300 h, and then they showed a slight decrease at 1900 h (Fig. 2B). There was a clear peak of abundance at 0700 h for Coleoptera, Araneae, Formicidae, and Diplopoda in the litter habitat, whereas Chilopoda did not appear (Fig. 2C).

There were six taxa that appeared only in *M. robusta*, four of which were registered at all times (Thomisidae 10: Araneae, *Phlegyas* sp.: Hemiptera, Armadillidiidae 2: Isopoda, *Blatta* sp.: Blattodea), and two of which were registered at three times (*Novalene* sp.: Araneae and *Dinocheirus tenoch* Chamberlin 1929: Pseudoscorpiones). There were three exclusive taxa for the herbaceous stratum habitat, of which only Cicadellidae 10 (Homoptera) was present at all times. In the litter habitat, Chrysomelidae 12 (Coleoptera) was present at almost all times, except at 1300 h.

Sphenarium purpurascens Charpentier 1842 (Orthoptera), *Crematogaster* sp. (Formicidae), and Melyridae 14 (Coleoptera) were registered on *M. robusta* and in herbaceous patch habitats. Polydesmida 3 (Diplopoda), *Paratrechina* sp. (Formicidae) and Coleoptera 41 were registered on *M. robusta* and in litter habitats. There were no taxa found both on herbaceous patches and in litter habitats; there were no fauna that used all three kinds of habitats.

PCA shows that the arthropod communities have more similarity in their assemblage by the type of habitat (*M. robusta*, herbaceous stratum, and litter) (Fig. 3) than by the time of collection (0100 to 0300 h, 0700 to 0900 h, 1300 to 1500 h and 1900 to 2100 h) (Fig. 4).

The highest Jaccard similarity index among arthropod communities within *M. robusta* at different local times was between 0700 h and 1700 h, and the lowest was between 0100 h and 1300 h (Table 1). The average of all similarity indices was 0.59 (± 0.04 SE).

	Local solar time (h)		
	0100	0700	1300
0700	0.603		
1300	0.448	0.566	
1900	0.673	0.717	0.518

Table 1. Jaccard similarity indices among arthropod communities within *M. robusta* at different local times solar hours (0100, 0700, 1300, 1900). Collection: July 2006, Reserva Ecológica del Pedregal de San Ángel, Mexico City.

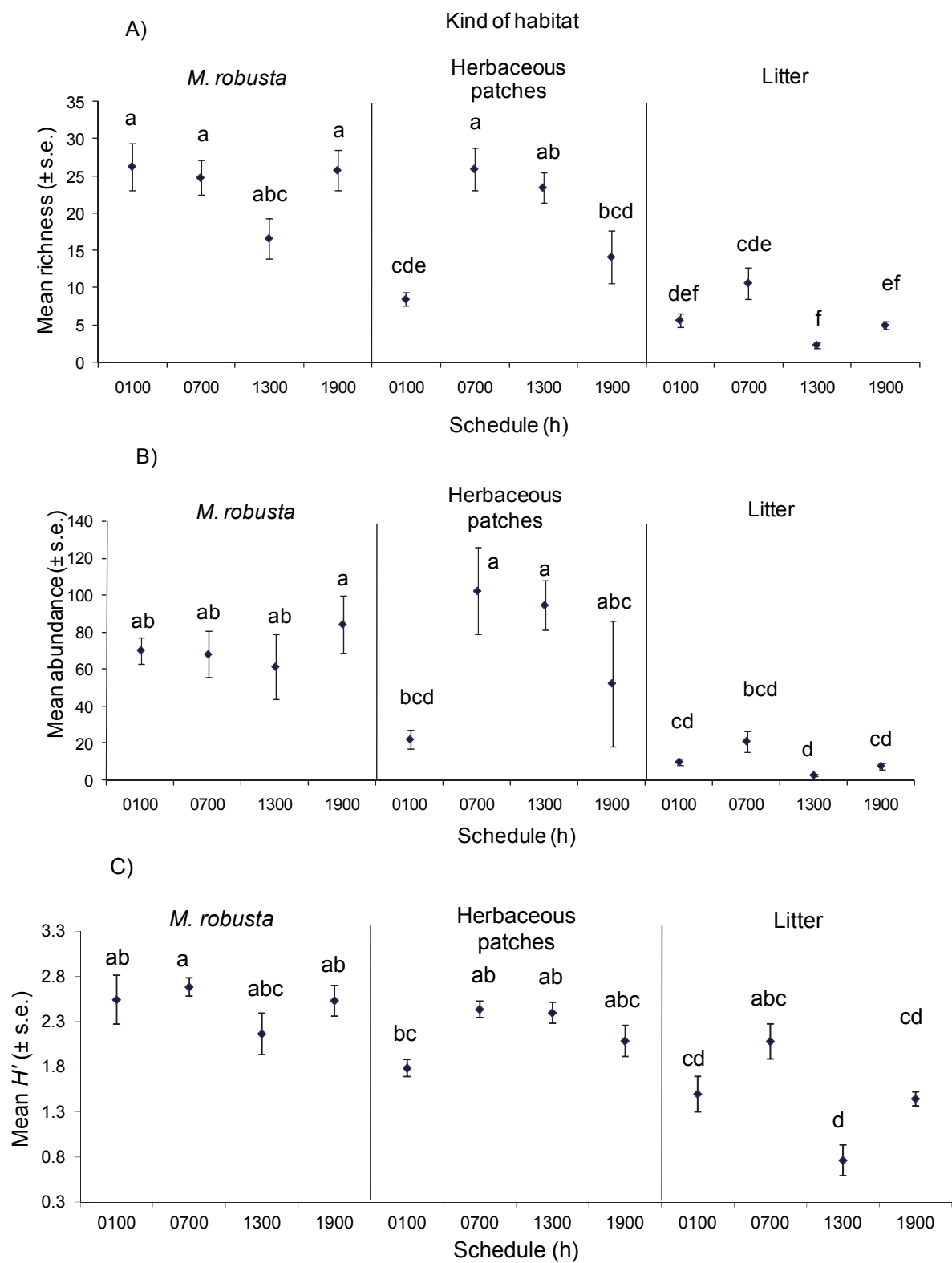


Fig. 1. Arthropod-fauna average richness (A), abundance (B), and index of diversity (C) (H') in three different kinds of habitats (*M. robusta*, herbaceous patches and litter) during four different sampling times (0100, 0700, 1300, 1900 h). Collection: July 2006, Reserva Ecológica del Pedregal de San Ángel, Mexico City. Letters denote significant differences ($\alpha=0.05$). Values are means \pm SE

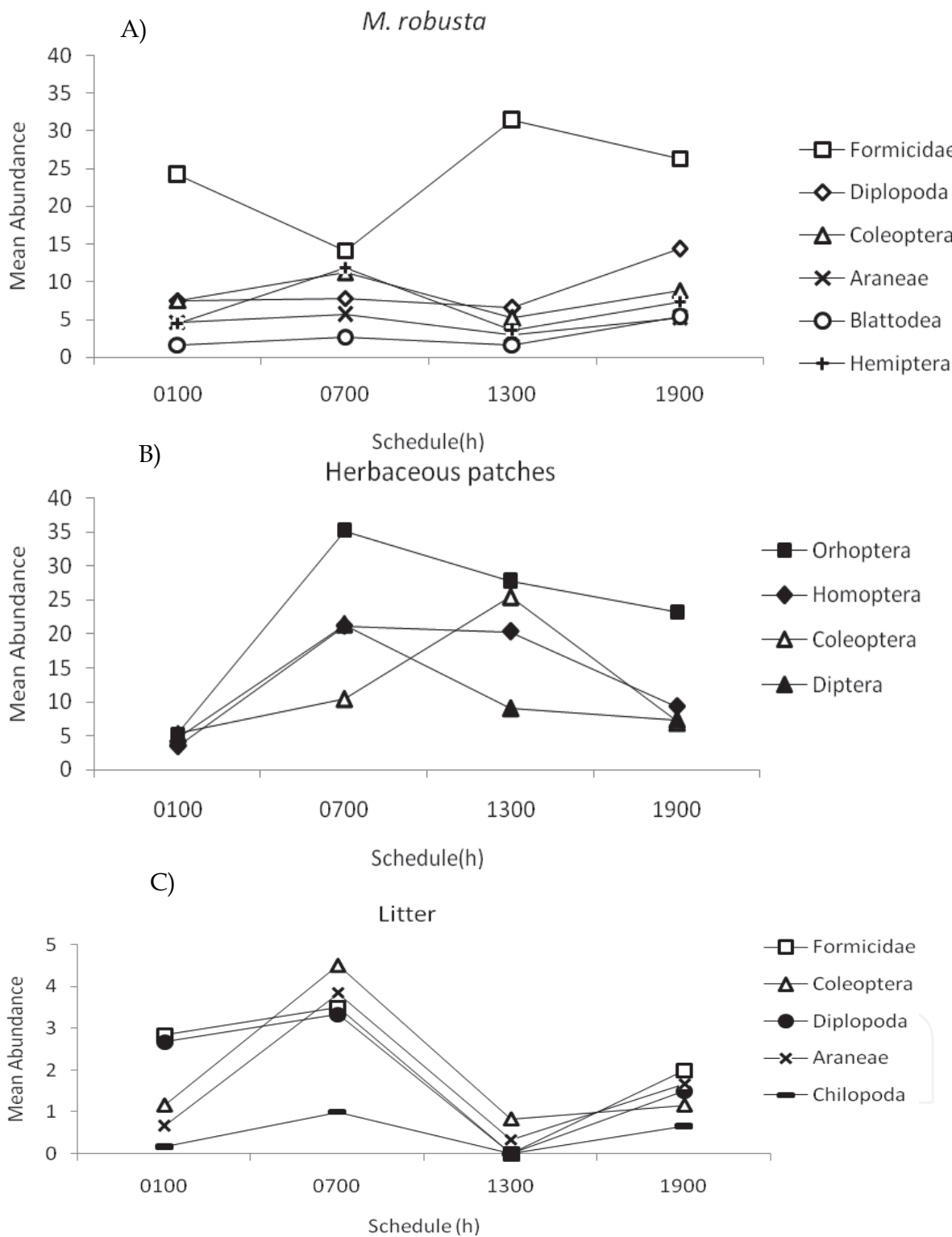


Fig. 2. Taxonomic group mean abundances during four different schedules (0100, 0700, 1300, 1900 h) in three different habitats: *Muhlenbergia robusta* (A), herbaceous patches (B), and litter (C). For the *M. robusta* and herbaceous patches habitats, only the taxonomic groups with an average abundance of greater than 5 are shown. Collection: July 2006, Reserva Ecológica del Pedregal de San Ángel, Mexico City

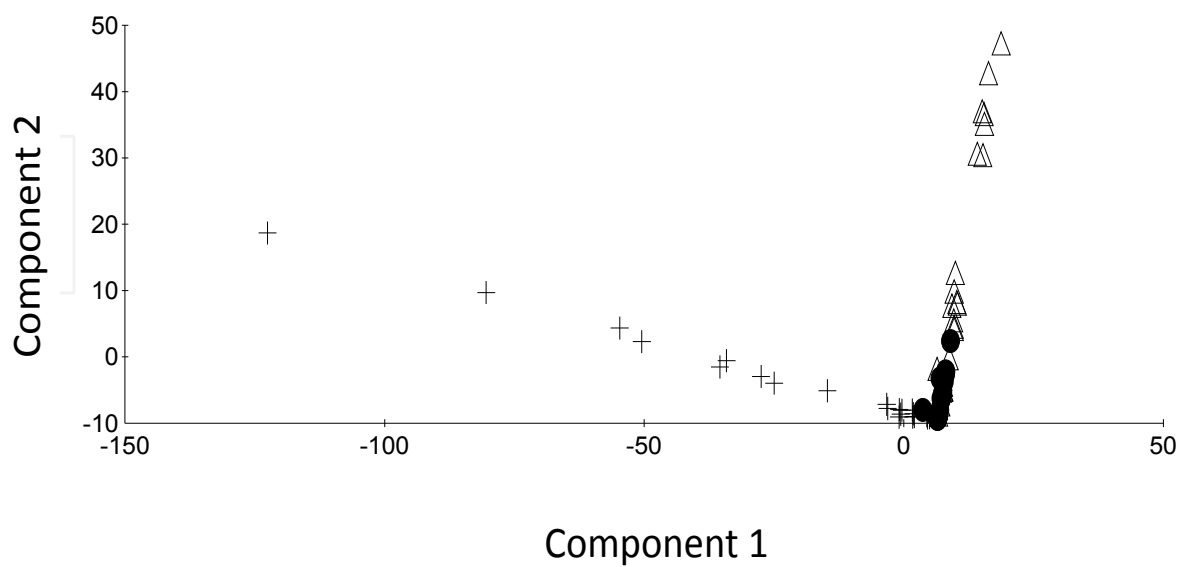


Fig. 3. PCA diagram that shows the arthropod communities of three kinds of habitats: *M. robusta* (+), herbaceous patches (Δ) and litter (●). Collection: July 2006, Reserva Ecológica del Pedregal de San Ángel, Mexico City

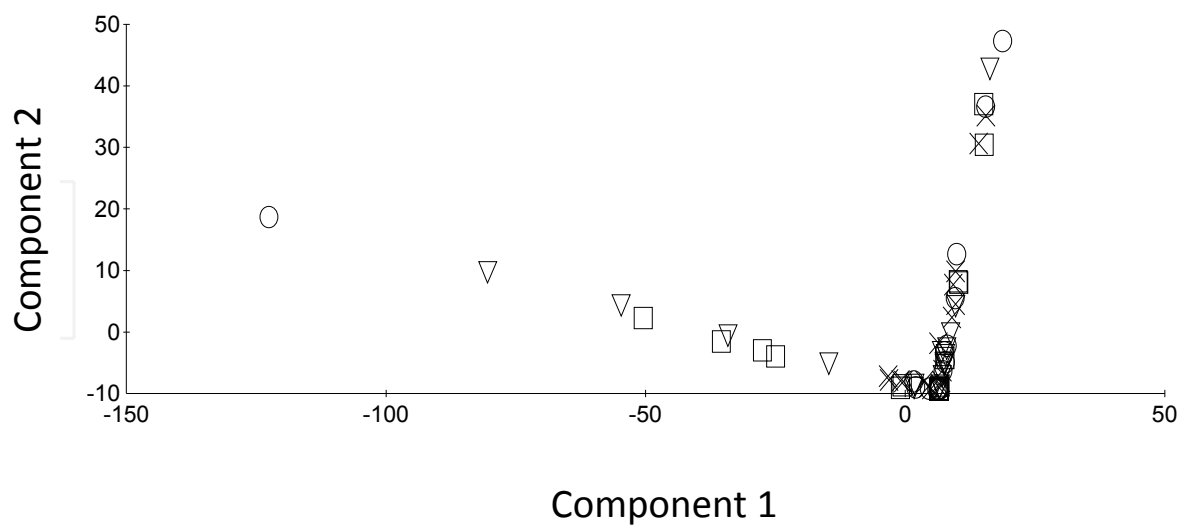


Fig. 4. PCA diagram that shows the arthropod communities at four times throughout the day: 0100 to 0300 h (x), 0700 to 0900 h (▽), 1300 to 1500 h (□) and 1900 to 2100 h (○). Collection: July 2006, Reserva Ecológica del Pedregal de San Ángel, Mexico City

Canfield's method showed that *M. robusta*'s presence was the most dominant at the site of the study. Following that, in order of importance, were the herbaceous patches, litter, exposed rock, and finally, shrubbery and trees (Fig. 5).

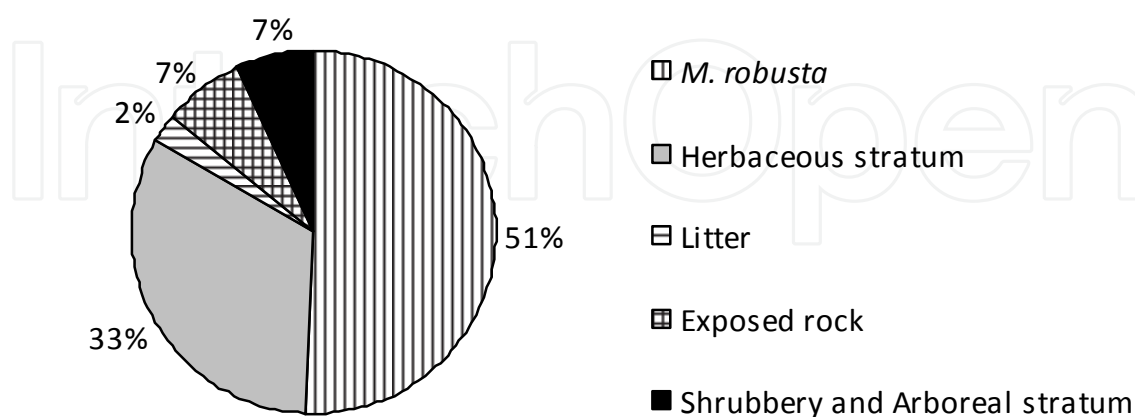


Fig. 5. Relative coverage of *M. robusta* and landscape elements (herbaceous patches, litter, exposed rock, and shrubbery and tree plants) in a sunny location at the Reserva Ecológica del Pedregal de San Ángel, Mexico City. Collection, August 2007

4. Discussion

Only 4.3% of the arthropod taxa (six morphospecies) were specialised on *M. robusta* in the use of habitat, which suggests that they carry out most of their activities (foraging, hiding and meeting) within this grass. These specialist arthropods showed the main functional groups in an ecosystem: herbivorous (*Phlegyas* sp.: Hemiptera), saprophagous (Armadillidiidae 2: Isopoda and *Blatta* sp.: Blattodea) and predatory (Thomisidae 10: Araneae, *Novalene* sp.: Araneae and *Dinocheirus tenoch*: Pseudoscorpiones). This suggests that grass conditions offer most of the requirements of these taxa in a microhabitat, i.e., alternative prey or food resources and refuge from predation.

Study results indicate that *Phlegyas* sp. (Hemiptera) could be a probable phytophagous specialist feeding on this grass. As the literature has reported, herbivorous insects are very specialised in the selection of their food (Bernays & Graham, 1988). The three predators with significant habitat specialisation on grass (Thomisidae 10: Araneae, *Novalene* sp.: Araneae and *Dinocheirus tenoch*: Pseudoscorpiones) show signs that the *M. robusta* structure facilitates their hunting strategies and provides suitable refuge for avoiding predation (Langellotto & Denno, 2004). It was observed that the habitat structure of the host plant can influence a community of spiders in plants. This was shown through a robust pattern of growth in the natural enemies of arthropods (hemipterans, mites, parasitoids and spiders) in complex structural habitats. These complex habitats provide a broad range of favourable conditions that attract natural enemies and decrease the need to move in search of more suitable conditions (Sunderland & Samu, 2000). In the same way, the two saprophagous taxa specialists on *M. robusta* (Armadillidiidae 2 and *Blatta* sp.) indicate that the layer of dead

organic matter typical on *M. robusta* (located in its base at ground level) could be an appropriate source of food and protection against predators (Jabin et al., 2004; Schmidt et al., 2005).

Most of the arthropod community taxa within *M. robusta* (i.e., 133 morphospecies) were generalised in their use of the different available herbaceous habitats. This could be attributed to the great variety of life forms and requirements that are characteristic of the Phylum Arthropoda. These organisms can be categorised as (1) taxa with a regular association with *M. robusta* and (2) taxa that use *M. robusta* and other herbaceous habitats.

One example of a taxon with a regular association with this grass could be *Sphenarium purpurascens* (Orthoptera), a grasshopper that eats the pollen and fruit of *M. robusta* (Mendoza & Tovar-Sánchez, 1996). Results show that this orthopteran was found in herbaceous patches at all times but was recorded in *M. robusta* only at 1300 h. This grasshopper likely forages on the reproductive structures of the grass only at this specific hour of the day because of favourable environmental conditions, as has been recorded for other floral visitors in this ecological reserve (Figueroa-Castro & Cano-Santana, 2004).

As an example of a taxon that uses *M. robusta* along with other herbaceous habitats, *Polydesmida 3* (Diplopoda) was registered in the grass at all times and in the litter habitat at three times. This can be interpreted to mean that saprophagous insects use these two habitats simultaneously because they offer food and refuge against adverse conditions. Other studies have also registered a direct relationship between saprophagous abundance and the amount of litter available (Jabin et al., 2004; Schmidt et al., 2005).

Apparently, there is no taxon that uses all three kinds of habitats. However, there are arthropods that likely use all of the described habitats. Of these, most are probably fliers. Unfortunately, their numbers could not be recorded because of their high mobility and the limitations of our sampling techniques.

The *M. robusta* habitat had the greatest coverage of all the landscape types (51%), which explains the richness and abundance of the arthropods (139 taxa and 1529 individuals) found within this habitat. This landscape provides a greater quantity and variety of habitats as well as resources for the fauna. Similarly, species-area relationship (SAR) has described a direct link between the richness of arthropods and the extension of their host plant distribution (Lawton, 1978; Marshall & Storer, 2006; Ozanne et al., 2000; Southwood et al., 1982).

Despite the low coverage (33%) of the herbaceous patches, this habitat shows the highest arthropod richness (150 taxa) in comparison with the other two kinds of habitats. This could be because the herbaceous patches habitat comprises many species of plants that offer a greater variety of habitats and food for the arthropod community; this permits the establishment of more species with diverse requirements (Symstad et al., 2000).

Results show that the structure of the arthropod community within *M. robusta* is constant throughout the day, based on (1) the richness and abundance per plant and the diversity (H') and (2) the stable abundances of the principal taxonomic groups within the grass throughout the day. However, Jaccard indices and PCA indicate that arthropod communities' assemblages change throughout the day (Fig. 4). This suggests that all of the available habitats for arthropods in *M. robusta* are fully occupied all day long and that arthropod communities within *M. robusta* have a particular assemblage with a remarkable turnover of species (41%).

PCA indicates that those arthropod communities within *M. robusta* present a remarkably different species composition compared to herbaceous patches and litter habitats. This could be explained because *M. robusta* offers diverse (1) microclimatic conditions, (2) types of resources and (3) interactions with other species. These factors are decisive in determining the establishment of species (Begon et al., 2006).

In the herbaceous patches habitat, arthropod richness and abundance—and the abundance of the principal taxonomic groups—showed a sudden increase at 0700 h. Following that, the recorded numbers decreased gradually. This indicates that arthropods experience a peak of activity at 0700 h in this habitat. These results agree with a study of arthropod floral visitor activity of four Compositae plants (*Eupatorium petiolare*, *Dahlia coccinea*, *Tagetes lunulata* and *Verbesina virgata*) in the REPSA (Figueroa-Castro & Cano-Santana, 2004). These authors found that the highest frequency of visits of anthophilous arthropods was between 0845 and 1645 h. The number of arthropod visitors on flowers was related to higher temperatures and lower relative humidity levels, which is directly related to arthropods' physiological responses to the environment.

In comparison to other habitats, the litter habitat showed the lowest richness, abundance, and diversity. This may be true because, for the majority of the arthropod community, this habitat is used only as a pass-through location for dispersion; the results show that the peak of arthropod mobility is at 0700 h. Moreover, this habitat represents an exposed location to predators because of the absence of vegetation; nevertheless, records indicate that it could be an appropriate habitat for saprophagous arthropods. Another reason could be the differences in the sample techniques for arthropod collection. The sample sizes for the three techniques were designed to achieve equality between them, but the lower records for the litter habitat could signify that the sample size should have been bigger for this habitat.

We are conscious that our results have limitations in their interpretation because of the difficulty in comparing these arthropod communities from different habitats when different trapping techniques were used. However, this study provides an approach to determining the level of specialisation of the arthropod community to a host plant and shows the diurnal dynamics of the whole arthropod community within a plant; both of these aspects of arthropod ecology have been little studied. For future studies that will try to corroborate our records, it may be appropriate to use an identical trapping technique on each of the treatments, if possible.

5. Conclusions

We conclude that the ratio of arthropod species with a high level of specialisation in the use of the *M. robusta* host plant was very low (4.3%). Furthermore, the structure of the arthropod community (richness, abundance, and index of diversity) in the grass was constant throughout the day, although the diurnal variation in the community assemblage shows a remarkable change (41%).

6. Acknowledgements

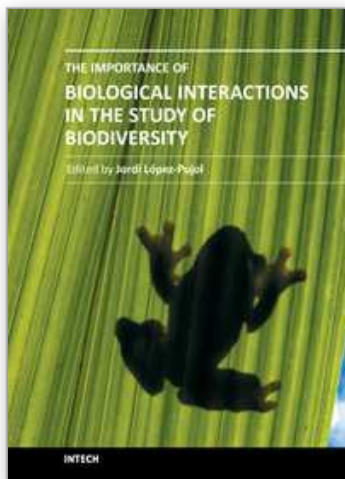
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The term biodiversity defines not only all the variety of life in the Earth but also their complex interactions. Under the current scenario of biodiversity loss, and in order to preserve it, it is essential to achieve a deep understanding on all the aspects related to the biological interactions, including their functioning and significance. This volume contains several contributions (nineteen in total) that illustrate the state of the art of the academic research in the field of biological interactions in its widest sense; that is, not only the interactions between living organisms are considered, but also those between living organisms and abiotic elements of the environment as well as those between living organisms and the humans.

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